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A Statistical Analysis of Volumetric Variation in the Neurocranium

By

Yuji Mizoguchi

Department of Anthropology, National Science Museum, Tokyo

Abstract In order to examine whether some parts of the neurocranium are more significant than others in adaptive sense, the approximate volumes for the eight regions of the neurocranium, *i.e.* right and left frontal, parietal, temporal and occipital, were first calculated on 43 early modern Japanese skulls, and coefficients of variation for the cubic roots of these volumes were estimated. They showed that the variations in the occipital portions were greater than those in the others. The correlation coefficients between right and left parts suggested that there were greater asymmetries in the temporal and occipital regions than in the frontal and parietal regions. A principal component analysis of these data revealed that the occipital regions varied relatively independent of the other regions. The adaptive significance for these features of variations in the neurocranium was discussed.

If a character is more important than other characters for the existence of the species which has them, the variation of the character with more adaptive significance is expected to be smaller than those of others. The lower variabilities of the human canines and first molars (Dahlberg, 1945; Mizoguchi, 1977, 1983), for example, imply that they have been more significant than the other teeth in the process of adaptation to environments. A purpose of the present study is to find whether or not there is any differential pattern of variation among regions of the neurocranium, as in the dentition.

Many authors have studied the size and shape of the human skull from various viewpoints. Among others, Howells (1957) examined the variation of the cranial vault in detail by the method of factor analysis using 54 linear measurements of the fractionized parts of the cranial vault. Kanda (1973), based on lateral cephalograms of the skulls, analyzed the relations between the maximum cranial length and 42 other antero-posterior linear lengths of small parts on the median sagittal plane by the factor analysis method. Benfer (1975) and Kanazawa (1980) extracted some common factors accounting for the variations of three dimensional coordinates of cranial landmarks by the principal component analysis method. Most of these studies on the cranial variation, however, have been based on linear measurements or distances. The present investigation attempts to reduce the number of the variables, avoiding loss of information, in order to obtain clear-cut results. This may be accomplished by analyzing volumes of fractionized parts instead of linear measurements. The results obtained in this way will be compared with previous studies, and the morphological variation in the neurocranium will be discussed from a viewpoint of adaptation.

Materials

Forty-three skulls of early modern Japanese males from the final Edo period were used. They were collected by Emeritus Prof. H. SUZUKI of the University of Tokyo. Measurements of these skulls were carried out by the present author.

Methods

Method for obtaining the volumes of polyhedra

The neurocranium was subdivided into eight regions, *i.e.* frontal, parietal, tem-

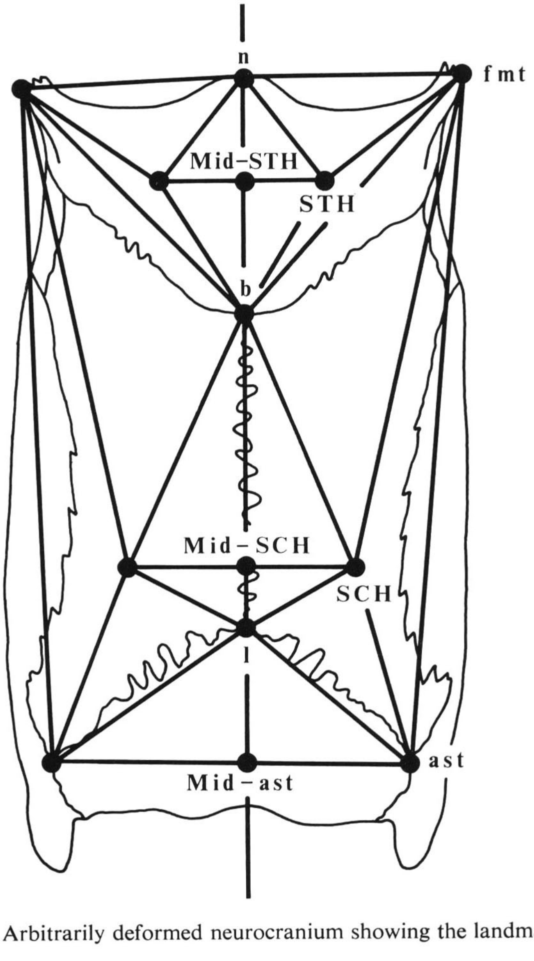

Fig. 1. Arbitrarily deformed neurocranium showing the landmarks used.

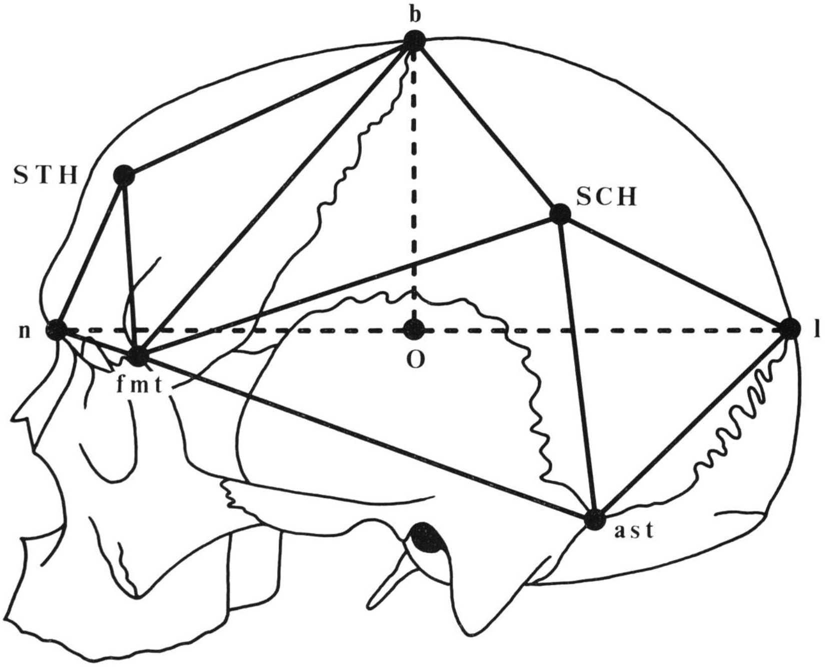

Fig. 2. Landmarks on the neurocranium (lateral view).

poral and occipital regions on the right and left sides. This subdivision was performed based on eleven landmarks: *nasion* (*n*), *bregma* (*b*), *lambda* (*l*), right and left *frontomalare temporale* (*fmt*), right and left *asterion* (*ast*), right and left *STH*, and right and left *SCH* (Figs. 1 and 2). The landmarks *STH* and *SCH* were defined in this study. *STH* is the highest point of the frontal tuberosity, a landmark used when measuring *Oberer frontaler Querdurchmesser* (9(2), MARTIN und SALLER, 1957). Similarly, *SCH* is the highest point of the parietal eminence, a landmark used when measuring *Parietale Schaedelbreite* (8(1), MARTIN und SALLER, 1957). On the basis of the above landmarks, the central point (*O*) as well as Mid-*STH*, Mid-*SCH* and Mid-*ast* were further defined. *O* is the intersection of the line *n–l* with the vertical line to the line *n–l* from *b*. Mid-*STH*, -*SCH* and -*ast* are the intersections of the plane *n–b–l* with the lines *STH–STH*, *SCH–SCH* and *ast–ast*, respectively. The above eight portions of the neurocranium were approximately represented by the following polyhedra. That is to say, the polyhedron for the frontal region (right or left) consisted of four tetrahedra: *n–STH–fmt–O*, *n–STH–Mid-STH–O*, *b–STH*–Mid-*STH–O* and *b–STH–fmt–O*. The polyhedron for the parietal region was also framed by four tetrahedra: *b–fmt–SCH–O*, *b–SCH*–Mid-*SCH–O*, *l–SCH*–Mid-*SCH–O* and *l–SCH–ast–O*. The polyhedra for the temporal and occipital regions were the tetrahedra *fmt–SCH–ast–O* and *l–ast*–Mid-*ast–O*, respectively.

To calculate the volumes of such polyhedra, the three dimensional coordinates of cranial landmarks were determined in advance through measuring the distances from the three landmarks, *nasion*, *bregma* and *lambda*. Sliding and spreading calipers with an accuracy of 1 mm were used for these measurements. This method for determining the three dimensional coordinates of cranial landmarks is practically the same as that of BENFER (1975).

Methods of statistical analysis

Intraobserver error variances were estimated by the analysis of variance for one-way classification (KEMPTHORNE, 1969). To carry this out, all the skulls dealt with here were measured twice at an interval of about one year.

The variations of the eight regions in the neurocranium were compared with one another using the coefficient of variation, and the differences between the coefficients were statistically tested by LEWONTIN's (1966) method.

In order to examine the interrelations between the eight cranial regions, product–moment correlation coefficients were first estimated and, then, the principal component analysis (LAWLEY and MAXWELL, 1963; OKUNO *et al.*, 1971, 1976; TAKEUCHI and YANAI, 1972) was applied to the correlation matrix.

Methods of calculation

The statistical calculations were performed by the HITAC M-280H System of the Computer Centre, University of Tokyo. The programs used are THRCRM for three dimensional coordinates and the volumes of polyhedra, MIVCRL for the analysis of variance for one-way classification, BSFMD for means, standard deviations and coefficients of variation, and PCAFPP for principal component analysis. All were written in FORTRAN by the present author.

Results

In this study, each region of the neurocranium was represented by the cubic root of its approximate volume. The intraobserver error variances for the cubic roots were confirmed to be small in general (Table 1), varying from 1.3 to 10.2% of the total variance (percent error variance $=100V_W/(V_W+(V_B-V_W)/2)$). In the succeeding analyses, the mean values of the repeated measurements on the same subjects were employed to minimize the effects of errors.

The means, standard deviations and coefficients of variation of the eight regions of the neurocranium are shown in Table 2. The difference between right and left portions was not significant at the 5% level in means nor in variances in any region. The coefficients of variation for the occipital regions were found to be significantly greater than those for the other regions (Table 3; Fig. 3).

Table 4 shows the product-moment correlation coefficients between the eight regions. From this, it is clear that the correlation between right and left portions in any region tends to be higher than those of the other combinations. In particular,

Table 1. Intraobserver error variances estimated for the cubic roots of volumes of the eight regions in the neurocranium.

Region (side)	Variance (d.f.)[1)		F-ratio
	Between classes (V_B)	Within classes (V_W)	
Frontal (R)	4.6449 (33)	0.0303 (34)	153.55*
(L)	4.1000 (40)	0.0502 (41)	81.68*
Parietal (R)	6.3221 (39)	0.3399 (40)	18.60*
(L)	6.8731 (38)	0.0924 (39)	74.41*
Temporal (R)	2.3896 (39)	0.0991 (40)	24.12*
(L)	2.9365 (40)	0.1313 (41)	22.37*
Occipital (R)	4.7353 (39)	0.0743 (40)	63.70*
(L)	4.0976 (39)	0.0506 (40)	80.95*

1) From the analysis of variance for one-way classification.
* $P<0.005$, by one-tailed F-test.

Table 2. Means, standard deviations and coefficients of variation of the cubic roots of volumes of the eight regions in the neurocranium in Japanese males.

Region (side)	Sample size	Mean (in mm)	Standard deviation	Coef. of variation
Frontal (R)	34	44.1	1.5	3.5
(L)	41	43.5	1.4	3.3
Parietal (R)	40	57.4	1.8	3.1
(L)	39	57.0	1.9	3.3
Temporal (R)	40	42.0	1.1	2.6
(L)	41	41.7	1.2	2.9
Occipital (R)	40	33.1	1.5	4.7
(L)	40	33.0	1.4	4.3

the right-left correlations of the frontal and parietal regions were found to be the highest and significantly higher than those of the temporal and occipital regions at the 0.1% level (Table 5).

The principal component analysis of the correlation matrix on the neurocranium (Table 4) showed that the first principal component was highly correlated with the frontal, parietal and temporal regions, while the second principal component was, roughly speaking, correlated with the occipital regions alone (Table 6; Figs. 4 and 5). This means that the occipital regions vary largely independent of the other regions in the neurocranium. It should be further pointed out that the communalities of the temporal regions were relatively low (Table 6). This implies that the temporal regions vary relatively independent of the other regions except that they are influenced by the general size factor, *i.e.* PC I. On the other hand, it is clear that the frontal and parietal regions are somewhat correlated with each other even after the influence of the general size factor has been excluded from their variation (Table 6; Fig. 5).

Table 3. Significance tests for the differences between the coefficients of variation by LEWONTIN's (1966) approximation method.

	F-value							
	1	2	3	4	5	6	7	8
1. Frontal (R)								
2. (L)	1.11							
3. Parietal (R)	1.25	1.13						
4. (L)	1.13	1.02	1.10					
5. Temporal (R)	1.77*	1.60	1.42	1.56				
6. (L)	1.42	1.28	1.14	1.25	1.25			
7. Occipital (R)	1.81*	2.00**	2.25**	2.05**	3.20***	2.56***		
8. (L)	1.57	1.73*	1.95**	1.77*	2.77***	2.22**	1.15	

* $P<0.10$; ** $P<0.05$; *** $P<0.01$, by two-tailed *F*-test.

Table 4. Correlation coefficients between the eight regions in the neurocranium[1].

	1	2	3	4	5	6	7	8
1, Frontal (R)								
2. (L)	.98 (34)***							
3. Parietal (R)	.63 (34)***	.62 (39)***						
4, (L)	.57 (34)***	.57 (39)***	.94 (39)***					
5. Temporal (R)	.63 (34)***	.67 (39)***	.55 (40)***	.42 (39)**				
6. (L)	.60 (34)***	.63 (41)***	.51 (39)***	.55 (39)***	.76 (39)***			
7. Occipital (R)	.03 (34)	.05 (39)	.13 (40)	.09 (39)	.45 (40)**	.53 (39)***		
8. (L)	.13 (34)	.13 (39)	.09 (40)	.13 (39)	.36 (40)*	.61 (39)***	.83 (40)***	

[1] The number in parentheses is the sample size for the relevant pair of characters.

* $P<0.05$; ** $P<0.01$; *** $P<0.001$.

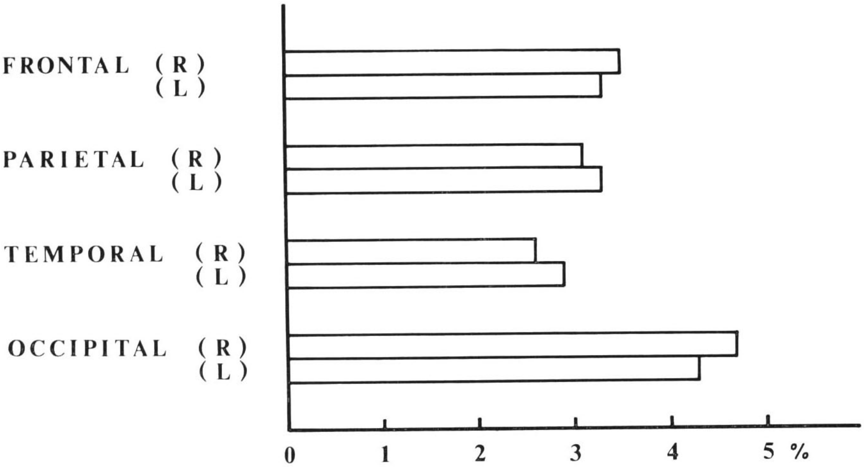

Fig. 3. Coefficients of variation for the cubic roots of volumes of the eight regions in the neurocranium.

Table 5. Correlation coefficients between the right and left sides and the differences between them.

	Sample size	Correlation coefficient	Normal deviate between cor. coef.[1]
Frontal	34	.9791***	
Parietal	39	.9416***	
Temporal	39	.7596***	
Occipital	40	.8345***	
Frontal-Parietal			3.22**
-Temporal			7.76***
-Occipital			6.60***
Parietal-Temporal			4.61***
-Occipital			3.41***
Temporal-Occipital			1.20

[1] Normal deviates were estimated for the differences between correlation coefficients after FISHER's z-transformation (RAO, 1952; ANDERSON, 1958) was performed. One of two correlation coefficients observed was assumed to be a given correlation coefficient.

* $P<0.05$; ** $P<0.01$; *** $P<0.001$.

Discussion

There are two findings of particular importance. One is the greater and independent variability of the occipital region (Tables 3 and 6). The other is the right-left asymmetries in the temporal and occipital regions which are indicated by the lower correlation coefficients between the right and left sides (Table 5).

The greater variability of the occipital region is discernible also in the findings of

Table 6. Principal component analysis of the correlation matrix on the eight regions in the neurocranium.

Region (side)	Factor loading			Communality
	PC I	II	III	
Frontal (R)	0.83*	−0.35*	−0.34*	0.9366
(L)	0.85*	−0.33*	−0.36*	0.9579
Parietal (R)	0.80*	−0.34*	0.45*	0.9647
(L)	0.76*	−0.32*	0.54*	0.9799
Temporal (R)	0.83*	0.14	−0.24	0.7704
(L)	0.86*	0.30	−0.07	0.8384
Occipital (R)	0.42*	0.85*	0.12	0.9074
(L)	0.45*	0.82*	0.05	0.8763
Total contribution (%)	55.71	24.35	10.33	90.40
Cumulative prop. (%)	55.71	80.07	90.40	90.40

* Factor loading of greater than 0.30 in absolute value.

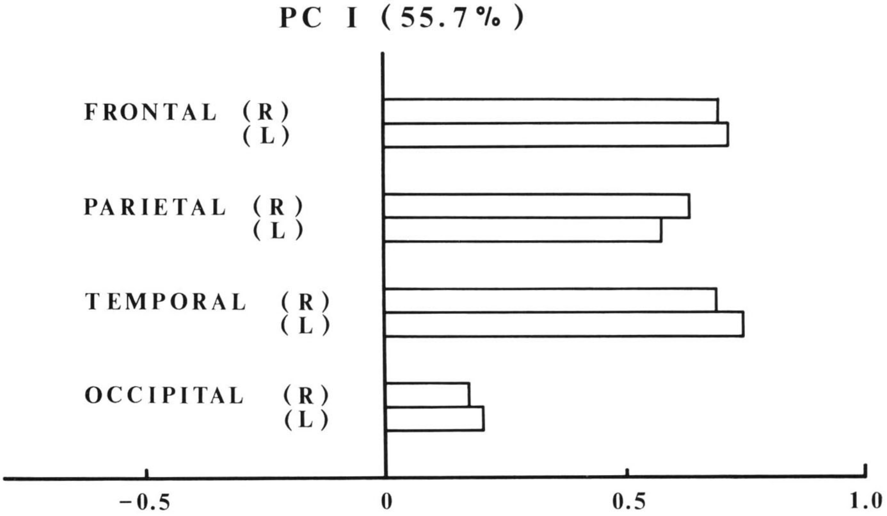

Fig. 4. Contribution, with the factor loading sign, of the first principal component to the standardized variance of each region.

previous works. Figs. 6 and 7 show the coefficients of variation for several cranial linear measurements in the modern Japanese (MORITA, 1950), early modern Japanese (SUZUKI *et al.*, 1962) and medieval Japanese (SUZUKI *et al.*, 1956), as well as in the average of 17 world-wide populations (HOWELLS, 1973). From these figures, it seems that there is no great difference in breadth between the occipital region and the other regions except for the Japanese females from the medieval period. However, there is a tendency for the occipital chord and subtense to vary more greatly than the frontal

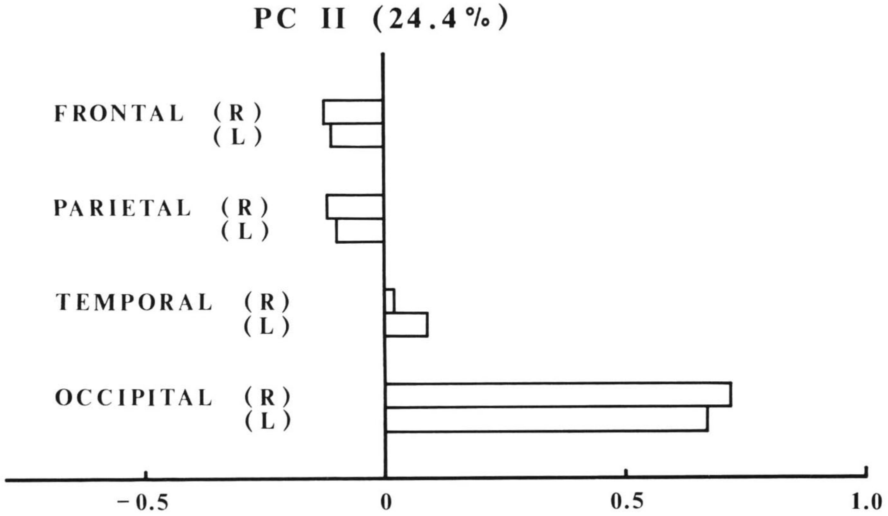

Fig. 5. Contribution, with the factor loading sign, of the second principal component to the standardized variance of each region.

and parietal chords and subtenses. This is compatible with the results of the present study.

The independence of the occipital region can also be found in previous works. HOWELLS (1957), based on 100 male skulls from Hythe, Kent, extracted a factor of general size and of 'dolichocephaly' from the variation in the cranial vault. This factor was correlated with the whole size, especially antero-posterior lengths, of the neurocranium and, at the same time, with the variables representing the backward prominence of occipital region. Similarly, KANDA (1968) examined the variations in two series of Japanese male skulls from Kinai and Tohoku, Japan, by factor analysis. In Kinai series, a factor which was highly related with the occipital arc, occipital chord and upper occipital arc was found to be somewhat correlated with the maximum cranial length and sagittal arc. In Tohoku series, it was found that there was a factor which was highly correlated with the occipital chord and slightly with the occipital arc and upper occipital arc. These factors on the occipital region were independent of a so-called general size factor in both series. From the findings of HOWELLS (1957) and KANDA (1968) as well as of the present study, it seems no doubt that the occipital region varies relatively independent of the other regions.

According to SJØVOLD (1984), it is within the bounds of possibility that a considerable part of the variation of the occipital region is due to genetic factors, while most of the variations of the frontal and parietal regions are caused by environmental factors (Table 7). In other words, it is likely that the frontal and parietal regions are genetically stable, but that the occipital region is genetically variable.

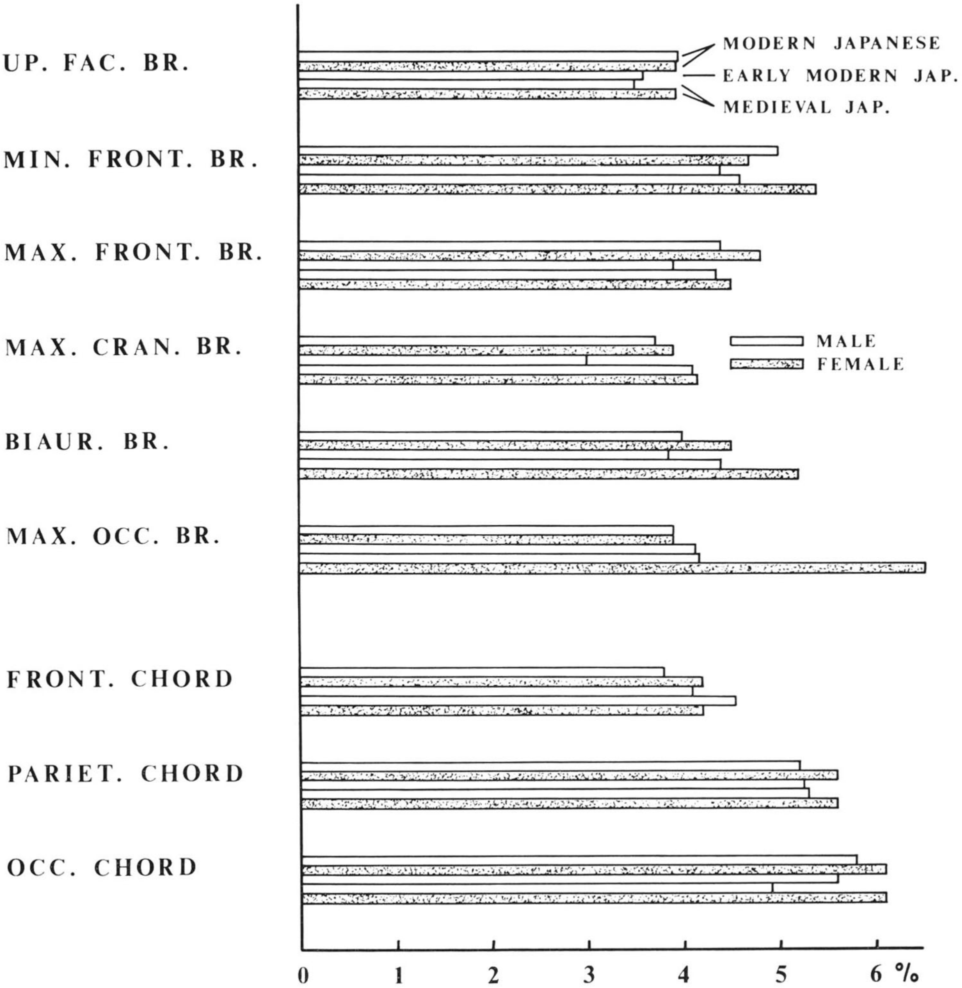

Fig. 6. Coefficients of variation for some cranial linear measurements. Source of data: MORITA (1950) for modern Japanese, SUZUKI *et al.* (1962) for early modern Japanese, and SUZUKI *et al.* (1956) for medieval Japanese.

If the variation observed on the external surface of the neurocranium is more or less respondent to the morphological variation of the brain, the greater, possibly genetic, variability of the occipital region should be interpreted to indicate the greater variability of the occipital lobe of the cerebrum, in which the visual area is located, or of the cerebellum. SCOTT (1957) considered that cranial form was determined largely by the growth pattern of the brain itself before the muscles had fully developed. According to SULLIVAN (1978), it is now accepted that sutural growth of the cranial bones is a secondary phenomenon, that is, increase in brain volume causes a potential separa-

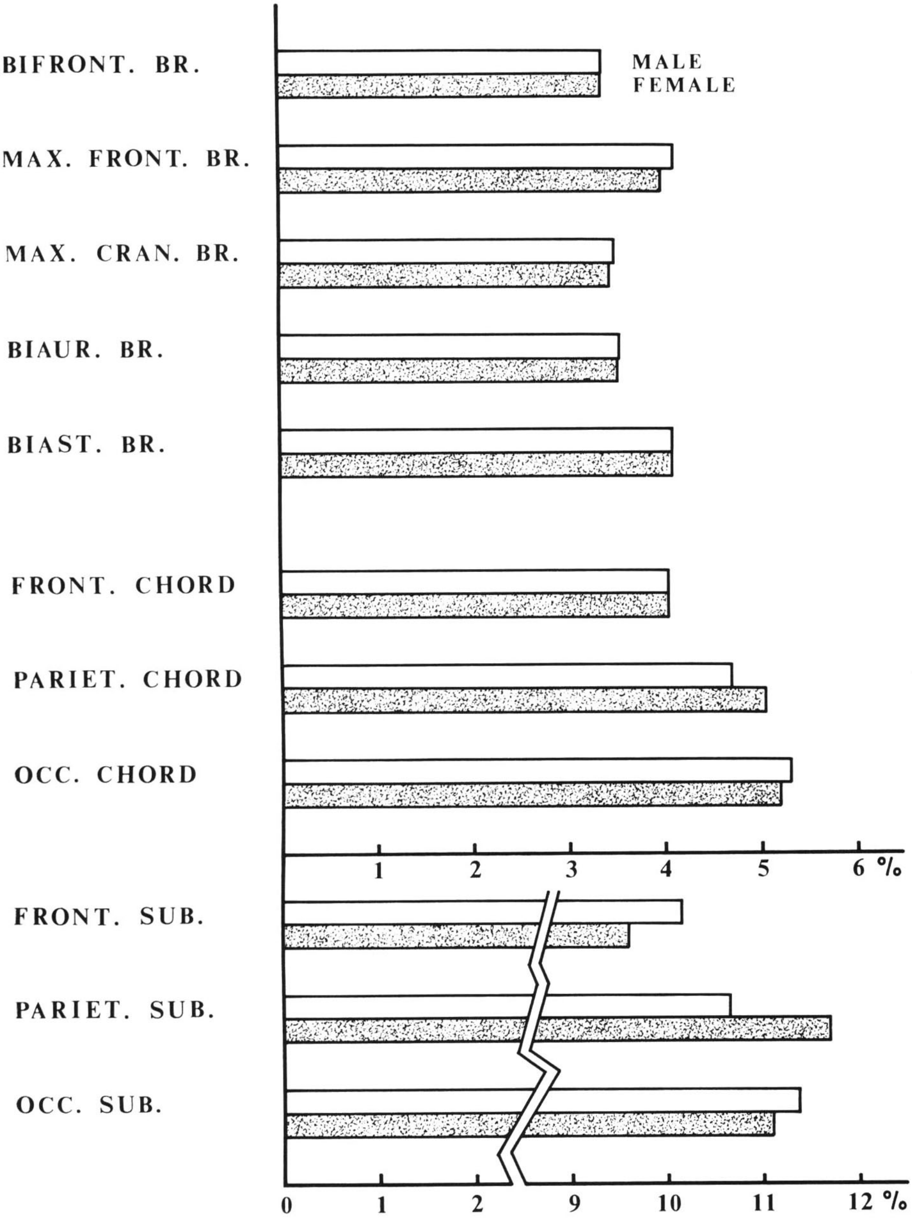

Fig. 7. Coefficients of variation for some cranial linear measurements in the average of 17 world-wide populations (Howells, 1973).

Table 7. Heritability estimates of some cranial measurements based on the parent-offspring relationships in Austria[1].

Items[2]	Heritability (No. of pairs)			
	Father		Mother	
	Son	Daughter	Son	Daughter
Frontal chord	.02 (54)	.33 (42)	.44 (56)	.09 (31)
Frontal subtense	.12 (54)	−.01 (42)	.10 (56)	−.03 (31)
Parietal chord	.47 (54)	.24 (42)	−.59 (56)***	.14 (31)
Parietal subtense	.38 (54)	.06 (42)	.38 (56)	.17 (32)
Occipital chord	.58 (52)***	−.01 (41)	.25 (56)	.28 (28)
Occipital subtense	.72 (53)***	.22 (40)	.52 (56)***	.03 (28)

[1] From SJØVOLD (1984).
[2] Measurement items defined by HOWELLS (1973).
* $P<0.05$; ** $P<0.025$; *** $P<0.01$.

tion of the bones at the sutures and, in turn, the separation is filled by bone formation at the sutures. If this is the case, it may be that the occipital lobe or the cerebellum or both of them have greater variability than the other parts of the brain and, therefore, less adaptive significance in modern man. However, MOORE (1967) reported that the length of the braincase in the masseterectomized rats, whose masseter muscles were ablated, was significantly smaller ($P<0.01$) than that in the control group whether adjusted values for differences in body weight were used or not. In the temporalectomized rats, the width of braincase was significantly larger ($P<0.001$) than in the control, though the values were not adjusted for differences in body weight. If these relations are applicable to the case of man, it is easy to suppose that variation of the muscular development has influence on variation of the cranial form in some degree. Therefore, morphological interrelations between the brain, the external surface of the neurocranium and the muscles attached to it need to be examined in more depth.

The lower correlations between the right and left sides in the temporal and occipital regions of the neurocranium (Table 5) imply that there are a considerable proportion of individuals who have asymmetries on the external surfaces of such regions. This phenomenon may also be associated with the morphological asymmetries in the corresponding parts of the brain, the asymmetries in development of the temporal and suboccipital muscles, *etc.* GESCHWIND and LEVITSKY (1968) reported that anatomical asymmetries between the upper surfaces of the human right and left temporal lobes were marked. GALABURDA *et al.* (1978) confirmed the great asymmetries in the human temporal lobes and further found that structural asymmetries between the hemispheres were also striking in both frontal and occipital lobes. Furthermore, there is evidence for the right-left asymmetry of the venous sinuses in the occipital portion (LE GROS CLARK, 1934; YAMAGUCHI, 1983). According to HOLLOWAY and DE LA COSTE-LAREYMONDIE (1982), the brain endocasts of modern *Homo sapiens* and other hominids (*Australopithecus*, *Homo erectus*, Neandertals) show a distinct left-occipital, right-frontal petalial pattern. A problem is how much the morphological variation of the brain affects the external variation of the braincase. In fact, despite of the findings by GALABURDA *et al.* (1978) and HOLLOWAY and DE LA COSTE-LAREYMONDIE (1982), the right-left correlation in the frontal region of the external surface was very high and the correlation between the right frontal and left occipital regions was not significantly different from zero in the present study (Table 4). This does not necessarily suggest that external asymmetries correspond to internal asymmetries.

To sum up, it was found that variation of the occipital region was relatively independent of and greater than those of the other regions of the neurocranium, and that there were greater right-left asymmetries in the temporal and occipital regions than in the other regions in some individuals. Interrelations between the variations observable on the internal and external surfaces of the neurocranium and those of the brain morphology should further be investigated in the future. However, it is most likely that the occipital region of the neurocranium is of less adaptive significance in modern man.

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